MORPHOLOGICAL AND ECOLOGICAL VARIATION ACROSS A HYBRID ZONE BETWEEN *ERYTHRONIUM OREGONUM* AND *E. REVOLUTUM* (LILIACEAE)

GERALDINE A. ALLEN and JOSEPH A. ANTOS
Department of Biology, University of Victoria,
Victoria, British Columbia V8W 2Y2, Canada

ABSTRACT

Erythronium oregonum and *E. revolutum* overlap only slightly in geographic distribution, but can hybridize where they co-occur. Morphological traits of *Erythronium* and cover of associated species were assessed in 1 m^2 plots in one hybrid and several pure populations of these two species on Vancouver Island. The species differ in size of flowers, relative size of scape and leaves, and several flower color characters. They also differ ecologically, *E. oregonum* occupying drier microsites than *E. revolutum*. Hybrids between them exhibited various recombinations of the parental morphological traits. Morphological variation in *Erythronium* at the hybrid locality was correlated with the ecological characteristics of the plots as indicated by a detrended correspondence analysis of associated plant species ($r = 0.64$). *Erythronium oregonum* and *E. revolutum* apparently are maintained as separate taxa by their ecological differences.

The genus *Erythronium* reaches its greatest diversity in western North America, where approximately 14 species occur (Applegate 1935, Hitchcock et al. 1969, Hammond and Chambers 1985). Although some of these have been studied ecologically (Caldwell 1969, Antos and Zobel 1984, Thomson and Stratton 1985), little is known about evolutionary relationships within the genus, or the genetic and ecological basis for species differences.

Erythronium oregonum Applegate and *E. revolutum* Smith are lowland species of the Pacific Northwest. They are morphologically and ecologically similar, and Applegate (1935) has reported hybrids between them. Both species have mottled leaves, small saccate appendages on the inner tepals, dilated anther filaments, and a three-lobed stigma. *Erythronium revolutum* has yellow anthers and rose pink tepals with yellow banding at the base. *Erythronium oregonum* is more variable; in many populations (including those in British Columbia) the anthers are yellow and the tepals are white with yellow and red banding at the base, but southern populations commonly have paler anthers and cream-colored tepals lacking the red markings. In this paper we describe an instance of hybridization between *E. oregonum* and *E. revolutum* in British Columbia, and present evidence concerning morphological and ecological differences between the two species.

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Methods

Study plots. Hybrids occurred with *E. oregonum* and *E. revolutum* at Skutz Creek (48°47′N, 123°57′W), a small tributary of the Cowichan River located 9.2 km east of Cowichan Lake on southern Vancouver Island, British Columbia. We established 29 1 m^2 plots at this site in areas of high *Erythronium* density. The plots were located to encompass the full range of variation in morphology and habitat of *Erythronium* at the site. For comparison, we located eight additional plots in pure populations of *E. oregonum,* of which five were along the Cowichan River (1.0 km downriver from Skutz Creek, 48°47′N, 123°56′W) and three were near Victoria (at Beaver Lake, 48°31′N, 123°23′W, and on the University of Victoria campus, 48°28′N, 123°19′W). We also located five plots in pure populations of *E. revolutum* along Sutton Creek (48°49′N, 124°13′W), 2.0 km west of Honeymoon Bay on Cowichan Lake.

Morphological characteristics. We measured eight morphological characters of taxonomic importance (tepal color, style color, stamen filament color, intensity of red banding on tepals, tepal length, length of dehisced anthers, scape height, and leaf length) on 25 plants in each of the 42 plots. Only characters that could be assessed nondestructively were used. Color intensities (hue and lightness) were determined using a Munsell color chart (Munsell Color, Baltimore, MD). We also calculated a derived character, scape-leaf ratio (=scape length/leaf length).

We used pure populations of *E. oregonum* and *E. revolutum* to establish mean values of the diagnostic characters of each species. The Cowichan River and Victoria populations of *E. oregonum* were not significantly different (t-test for each character, $p > 0.05$ in all cases), so the data from these were combined. We constructed a hybrid index using six characters (tepal color, style color, filament color, red banding, tepal length, and scape-leaf ratio) that differed significantly between the two species, but were not highly correlated with other characters. For all plants examined at the Skutz Creek hybrid locality, the values of each character were scaled between the mean values for *E. revolutum* (set at zero) and for *E. oregonum* (set at 10). Values outside the range of zero to 10 were set to zero or 10 as appropriate. A weighting factor inversely related to the amount of overlap between the pure populations was then applied to each character (weights were 1.000 for tepal color, 0.984 for style color, 0.887 for filament color, 0.930 for red markings, 0.720 for tepal length, and 0.645 for scape-leaf ratio). The hybrid index was calculated as the sum of these weighted values for the individual characters, and this sum was then scaled between zero and 60. We calculated a mean hybrid index for each plot in order to determine

TABLE 1. MEAN VALUES OF CHARACTERS USED IN STUDY OF *Erythronium oregonum* AND *E. revolutum*. Color traits are expressed as values on an integer scale; tepal, style, and filament color vary from 0 (white) to 7 (deep violet-pink), and red banding from 0 (absent) to 5 (broad deep-red bands). All characters differed significantly between the two species (t-test; p values given below).

	E. oregonum (n = 200)		*E. revolutum* (n = 125)		
Character	$\bar{x}$	s.d.	$\bar{x}$	s.d.	p
Tepal color	0.0	0.1	4.6	0.5	0.0001
Style color	0.0	0.0	3.4	1.3	0.0001
Filament color	0.2	0.9	3.7	1.8	0.0001
Red banding	2.2	1.2	0.0	0.0	0.0001
Anther length (mm)	6.6	1.1	6.2	0.9	0.0003
Petal length (mm)	44.7	5.0	37.0	2.9	0.0001
Leaf length (cm)	16.9	4.3	16.1	2.3	0.0253
Scape height (cm)	28.0	7.1	21.4	2.9	0.0001
Scape-leaf ratio	1.7	0.2	1.3	0.1	0.0001

whether plants in the plot were predominantly "*revolutum*", "*oregonum*" or "hybrid" in character.

Ecological characteristics. For all 1 m^2 plots except those at Victoria, we recorded the percent cover of each vascular plant and moss species present. All cover values were subjected to log transformation before analysis. We carried out detrended correspondence analyses of these data using the program DECORANA (Hill 1979) in order to assess ecological resemblance among the plots. The analyses were performed with all plots and with the Skutz Creek plots only, with and without tree species included. We then examined the relationship between *Erythronium* morphology, as indicated by the hybrid index, and ecological characteristics, as indicated by plot ordination scores derived from the detrended correspondence analysis.

RESULTS

Morphological characteristics. Populations of *E. oregonum* and *E. revolutum* differed in a number of the morphological characters examined (Table 1). The most striking differences between the two species are in tepal color and markings. Other differences, which were observed during this study but not measured, included (1) length of stigma lobes (shorter in *E. revolutum*); (2) curvature of tepals (much reflexed in *E. revolutum,* generally less so in *E. oregonum*); (3) anther position (connivent around the style in *E. revolutum,* spreading in *E. oregonum*); and (4) leaf position (generally more erect in *E. revolutum*).

We examined correlations among the characters in Table 1, first for all of the specimens measured at the Skutz Creek locality, and

TABLE 2. PERCENT COVER AND (IN PARENTHESES) PERCENT OCCURRENCE OF VASCULAR PLANT SPECIES IN PLOTS GROUPED BY THE *Erythronium* HYBRID INDEX. Included are all species with >5% cover in at least one group. T = <0.5% cover; nomenclature follows Hitchcock and Cronquist (1973).

Species	Hybrid Index		
	<10 (n = 6)	10–50 (n = 16)	>50 (n = 7)
Trees			
Alnus rubra	78 (100)	50 (94)	16 (57)
Abies grandis	2 (17)	8 (50)	0 (0)
Acer macrophyllum	11 (100)	27 (100)	29 (57)
Pseudotsuga menziesii	10 (17)	1 (19)	42 (86)
Shrubs			
Rubus spectabilis	32 (83)	22 (81)	1 (14)
Oemleria cerasiformis	8 (67)	9 (69)	11 (29)
Symphoricarpos albus	0 (0)	5 (31)	7 (43)
Holodiscus discolor	T (17)	T (6)	37 (57)
Herbs			
Trautvetteria caroliniensis	32 (83)	5 (38)	T (14)
Maianthemum dilatatum	13 (33)	10 (38)	1 (14)
Dicentra formosa	7 (33)	6 (50)	1 (14)
Tolmiea menziesii	2 (50)	13 (56)	T (14)
Heracleum lanatum	4 (50)	9 (31)	6 (29)
Viola glabella	T (17)	6 (50)	8 (43)
Cardamine pulcherrima	3 (17)	4 (38)	16 (86)
Perideridia gairdneri	0 (0)	0 (0)	9 (43)

secondly for that subset of specimens with a hybrid index between 20 and 40. In the first comparison some high correlations occurred between characters found together in the same species, particularly color characters. The highest correlation coefficient (0.78) was between tepal color and filament color. In the second comparison, which was restricted to clearly hybrid specimens, no correlation coefficient higher than 0.51 was obtained, and most were much lower.

Ecological characteristics. Results of the detrended correspondence analyses indicate that *E. oregonum* and *E. revolutum* differ in their ecological characteristics. The ordinations were all similar and the first axis in each case corresponded to a moisture gradient. At the hybrid locality typical *E. oregonum* was usually found on well-drained microsites underlain with shale, whereas typical *E. revolutum* was usually found on wetter microsites with black, humus-rich soils. Sample plots grouped on the basis of mean hybrid index into "*oregonum*", "*revolutum*" or "hybrid" differed substantially in species composition (Table 2). *Erythronium oregonum* typically grew in sites with a Douglas-fir canopy and sparse herbaceous understory;

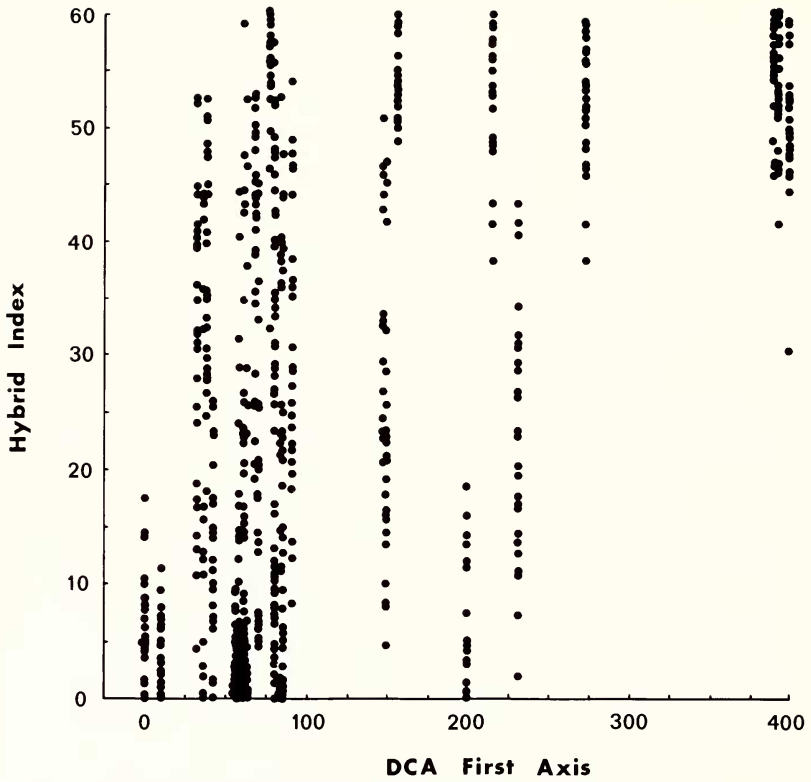

FIG. 1. Hybrid index of individual *Erythronium* in relation to their position on the first axis of a detrended correspondence analysis (DCA) of the 29 plots at Skutz Creek. The analysis was based on all associated species. Low scores on the DCA axis correspond to wetter sites and high scores to drier sites; typical *E. revolutum* has a hybrid index of zero, and typical *E. oregonum* a hybrid index of 60.

in contrast, *E. revolutum* was typically associated with luxuriant herb layers under a red alder canopy.

To examine relationships between morphological and ecological characteristics of *E. oregonum, E. revolutum* and their hybrids, we plotted the hybrid indices of all plants from the Skutz Creek locality against plot scores from the first axis of the detrended correspondence analysis (Fig. 1). The first DCA axis accounted for 57% of the variation in the species composition of the sample plots, and corresponded roughly to a moisture gradient with low scores indicating wetter sites and high scores indicating dry sites. Plots with low scores on the first DCA axis contained mainly *E. revolutum,* and those with high scores on this axis contained mainly *E. oregonum* (Fig. 1). The large amount of scatter in the central region of the figure indicates that *E. oregonum* and *E. revolutum* overlapped slightly in

their ecological tolerances, and also that the hybrid plants at Skutz Creek exhibited many combinations of morphological and ecological characteristics. Although the morphology of *Erythronium* plants varied greatly in plots located in intermediate habitat, 41% of the variation in mean hybrid index was related to position on the first DCA axis.

Discussion

The western North American species of *Erythronium* are largely allopatric in their distribution, and little quantitative information exists concerning the degree of interfertility and naturally occurring intergradation among species. Although only a few cases of hybridization between *E. oregonum* and *E. revolutum* have been reported (Applegate 1935), extensive hybridization can occur under appropriate conditions. The variety and abundance of intermediate forms found at the Skutz Falls study site suggest that many hybrid generations are present and that there is little or no post-zygotic reproductive isolation between the species, at least at this locality. Applegate (1935) considered these two species to be related closely on morphological grounds. Nevertheless, *E. oregonum* and *E. revolutum* are consistently different in a number of morphological characters as well as in their ecological requirements.

The evidence presented in this paper suggests that *E. oregonum* and *E. revolutum* maintain their distinct taxonomic characteristics largely through ecological separation. On Vancouver Island, *E. revolutum* typically occurs under deciduous trees on relatively wet sites such as stream terraces. It can be abundant, locally dominating the herb layer, but occurs on a restricted range of sites. *Erythronium oregonum* is most common on dry open sites such as forest openings and rock outcrops, although it occasionally occurs in wetter locations; it appears to occupy a wider variety of sites than *E. revolutum.* The overall geographic distributions of the two species reflect these ecological differences. *Erythronium revolutum* occurs on Vancouver Island and the adjacent mainland to the north, then south through the Olympic Peninsula of Washington and coastal regions of Oregon to northern California (Bierly and Stockhouse 1982, James 1983). Its occurrence is somewhat sporadic, probably reflecting relatively specific habitat requirements and the patchy distribution of suitable sites. *Erythronium oregonum* extends from the east coast of Vancouver Island and adjacent mainland British Columbia, southward through the Puget Trough of Washington and the Willamette Valley of Oregon (extending into the Coast Range and to the west slope of the Cascades); it reaches its southern limit in the vicinity of the Illinois River of southern Oregon (Applegate 1935).

Although the two species exhibit some overlap in range, they

seldom grow in close proximity because of their differences in habitat preference. For successful hybridization to occur, pollen or seeds must be transferred between parental populations. In *Erythronium,* this seems likely only if the two taxa are established immediately adjacent to one another. Such a situation exists at Skutz Creek, where dry slopes with fairly pure *E. oregonum* populations occur within 100 m of alluvial flats with populations of *E. revolutum.* Given the apparent absence of intrinsic genetic barriers between these two species, the close juxtaposition of divergent habitats that can support both taxa is probably the major reason for hybridization.

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